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# Experimental Tree Removal in Tallgrass Prairie: Variable Responses of Flora and Fauna along a Woody Cover Gradient

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# Experimental tree removal in tallgrass prairie: variable responses of flora and fauna along a woody cover gradient

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*Abstract*. Woody plant encroachment is a worldwide phenomenon in grassland and savanna systems whose consequence is often the development of an alternate woodland state. Theoretically, an alternate state may be associated with changes in system state variables (e.g., species composition) or abiotic parameter shifts (e.g., nutrient availability). When state-variable changes are cumulative, such as in woody plant encroachment, the probability of parameter shifts increases as system feedbacks intensify over time. Using a Before–After Control–Impact (BACI) design, we studied eight pairs of grassland sites undergoing various levels of eastern redcedar (*Juniperus virginiana*) encroachment to determine whether responses of flora and fauna to experimental redcedar removal differed according to the level of pretreatment redcedar cover. In the first year after removal, herbaceous plant species diversity and evenness, woody plant evenness, and invertebrate family richness increased linearly with pretreatment redcedar cover, whereas increases in small-mammal diversity and evenness were described by logarithmic trends. In contrast, increases in woody plant diversity and total biomass of terrestrial invertebrates were accentuated at levels of higher pretreatment cover. Tree removal also shifted small-mammal species composition toward a more grassland-associated assemblage. During the second year postremoval, increases in herbaceous plant diversity followed a polynomial trend, but increases in most other metrics did not vary along the pretreatment cover gradient. These changes were accompanied by extremely high growing-season precipitation, which may have homogenized floral and faunal responses to removal. Our results demonstrate that tree removal increases important community metrics among grassland flora and fauna within two years, with some responses to removal being strongly influenced by the stage of initial encroachment and modulated by climatic variability. Our results underscore the importance of decisive management for reversing the effects of woody plant encroachment in imperiled grassland ecosystems.

*Key words: alternate states; BACI design; eastern redcedar; grassland;* Juniperus virginiana; *land management; Oklahoma; succession; woody encroachment*.

## Introduction

Woody encroachment in grassland and savanna ecosystems is a worldwide phenomenon (Moleele and Perkins 1998, Silva et al. 2001, Briggs et al. 2005, Fensham et al. 2005) having significant implications from the perspectives of pastoral land management (Angassa 2005), endangered species preservation (Samson and Knopf 1994), and ecosystem biogeochemical processes (Schlesinger et al. 1990, Knapp et al. 2008). In North America, ecosystems in the arid and semiarid southwest (Archer 1989, Van Auken 2000), Pacific Northwest (Miller et al. 2000, Bates 2005), and Great Plains (Gehring and Bragg 1992, Hoch et al. 2002) have experienced substantial increases in woody plant cover. In each of these systems, junipers (*Juniperus* spp.) are either the dominant encroaching species or are indirectly involved in the encroachment process.

Eastern redcedar (*Juniperus virginiana*, hereafter redcedar) woodlands have replaced many of the mixed and tallgrass prairies that formerly dominated the Great Plains, and threaten the biotic integrity of these imperiled ecosystems (Briggs et al. 2005). A number of studies have described the consequences of an ecosystem shift from grassland to redcedar-dominated forests, which range from changes in composition and diversity of associated floral and faunal assemblages (Gehring and Bragg 1992, Horncastle et al. 2005) to a variety of biogeochemical changes. Abiotic changes include above-

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ground effects such as nitrogen and carbon accumulation in biomass and associated changes in foliar litter quantity and quality (i.e., lignin content) compared to grassland (Norris et al. 2001, 2007); belowground effects include decreases in soil temperature and soil respiration (Smith and Johnson 2004), redistribution of soil carbon inputs (Smith and Johnson 2003), and net accrual of soil organic carbon and nitrogen (Hibbard et al. 2001, McKinley and Blair 2008). The relocation and sequestration of nutrients to aboveground biomass may reduce soil reserves, and, combined with decreased soil respiration rates, lower nutrient availability (i.e., nitrogen) for associated vegetation, resulting in lower plant and consumer productivity. On the other hand, given greater nutrient accumulation and availability, encroachment could facilitate short-term soil fertilization, increasing productivity of flora and fauna. Despite the ubiquity of redcedar in Great Plains grasslands and its potential for rapidly altering grassland ecosystems (Hoch et al. 2002), relatively little is known about whether changes associated with redcedar encroachment constitute a conversion from a grassland to an alternate woodland state. In addition, experimental evidence is needed to determine whether the level of woody encroachment in grasslands acts to constrain and/or facilitate the return of grassland floral and faunal assemblages following tree removal, a common restoration practice in grasslands.

Beisner et al. (2003) described two ways in which a system may come to occupy an alternate state. The first involves alterations to "state variables" (e.g., species richness, relative abundance), whereas the second involves changes to system "parameters" (e.g., nutrient availability, soil organic carbon and nitrogen stores, radiant energy regime). Briske et al. (2006) placed this dichotomy into a management context by associating the former with reversible, biotic changes and the latter with abiotic changes that fundamentally alter the system on a management time frame (years to decades). Thus, systems that exhibit state-variable changes may be returned to their original configuration through restoration of historical disturbance regimes (e.g., prescribed fire), whereas systems having undergone certain types of parameter shifts with positive feedbacks between biotic and abiotic factors may have strong ecological resilience to returning to their original state (Suding et al. 2004). In addition, where systems exhibit state-variable changes that are cumulative, such as the herbaceous–woody floristic shift during woody plant encroachment, these changes may comprise parameter shifts as system feedbacks intensify over time (Schlesinger et al. 1990).

Mechanical tree removal is an obvious, albeit expensive, strategy aimed at restoring grassland systems in areas of woody plant encroachment (Wilson and Schmidt 1990). Tree removal has been associated with increased biomass and diversity of associated herbaceous plant assemblages (Rose and Eddleman 1994, Bates et al. 2000, Lett and Knapp 2005). Such responses might be expected given increases in soil nutrient availability and cycling commonly seen in areas of woody expansion (Schlesinger et al. 1990, Hibbard et al. 2001), and the increase in light availability following tree removal.

It remains unclear whether the stage of encroachment mediates the effectiveness of grassland restoration, and studies of removal effects have not explicitly considered the level of pre-removal woody cover. Early in the encroachment process, young redcedar trees with small stem diameters and heights (Owensby et al. 1973) are likely to have only limited shading effects on herbaceous vegetation, and in turn, on grassland fauna that rely on herbaceous vegetation for food and cover. As a result, redcedar removal at early stages of encroachment would be expected to quickly return the system to a pre-encroachment grassland state. However, at advanced stages of redcedar encroachment, larger trees will have created more pronounced shading effects, contributed more aboveground litter, and consequently, reduced plant species richness (Limb et al. 2010) and altered soil biogeochemistry (Norris et al. 2001, Smith and Johnson 2004, McKinley and Blair 2008). These changes could exert a strong bottom-up influence on the direction and scope of the recovery of herbaceous plants and associated fauna following redcedar removal.

Grassland systems are often characterized by their rapid responses to a suite of biotic and abiotic factors, and thus represent valuable systems for understanding community change. Our study examined the short-term capacity for experimental tree removal to restore tallgrass prairie undergoing woody encroachment. Many studies on the effects of woody encroachment have focused on the vegetation assemblage; few have examined the effects of encroachment on grassland fauna (Coppedge et al. 2001, Horncastle et al. 2005, Matlack et al. 2008). We used a modified Before–After Control–Impact design (BACI; Stewart-Oaten et al. 1986) (1) to examine concomitant responses of grassland floral and faunal (i.e., invertebrates, small mammals) assemblages to experimental redcedar removal, and (2) to determine whether the level of pretreatment redcedar cover modulated floral and faunal responses to tree removal in two years following treatment.

We predicted that experimental redcedar removal would increase floral and faunal diversity of removal sites above that of corresponding nonremoval sites, and compared three alternative outcomes for removal effects (Fig. 1). The first was that removal would increase diversity of grassland floral and faunal assemblages, and that similar effects would occur regardless of the pretreatment level of redcedar cover (Fig. 1A). This result would suggest that the changes caused by encroachment were common across all levels of pretreatment redcedar cover. The second possibility was that redcedar removal would increase floral and faunal diversity, but that the magnitude of these responses would increase linearly as a function of pretreatment redcedar cover (Fig. 1B). We also postulated a third

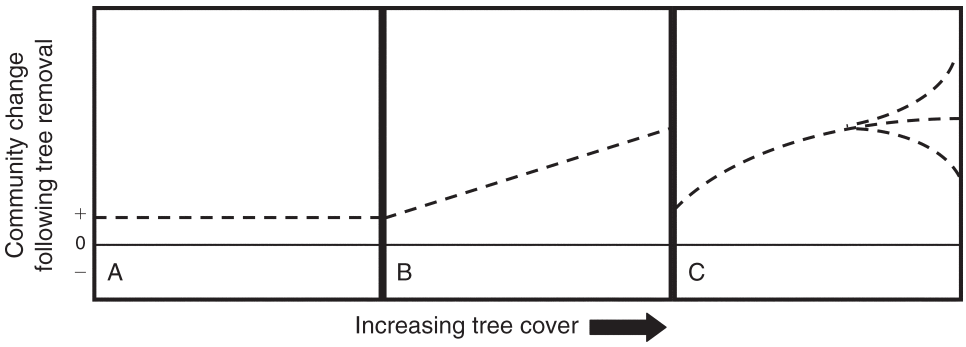


FIG. 1. Three conceptual models illustrating changes in floral and faunal assemblages at tree removal sites relative to corresponding nonremoval sites in tallgrass prairies of Oklahoma, USA. Proposed trends in the differences between removal sites (dashed lines) and nonremoval sites (solid lines) represent (A) responses to removal, (B) linear responses along the gradient of pretreatment redcedar cover, or (C) nonlinear responses to biotic–abiotic interactions along the gradient of pretreatment redcedar cover.

outcome in which floral and faunal responses to treatment would be nonlinear as a result of interactions between changes in state variables and system parameters (Fig. 1C).

## METHODS

### *Study system and experimental design*

Our study was conducted from 2005 to 2008 in tallgrass prairies ~18 km west of Stillwater (36°7′ N, 97°3′ W) in Payne County, Oklahoma, USA. The regional climate is humid continental with a mean annual temperature of 15°C and mean annual precipitation of 850 mm (Arndt 2004). Grasslands historically represented the dominant vegetation in the area; trees were generally restricted to patches of cross-timbers forest and riparian margins. Presently, grasslands sustain extensive livestock grazing, are burned irregularly, and exhibit increasing levels of woody vegetation. Herbaceous vegetation consists of such grasses as little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*), and an assortment of forbs. Redcedar is the dominant tree within the grasslands, with black jack oak (*Quercus marilandica*) and post oak (*Q. stellata*) being less common. In addition, shrubs such as buckbrush (*Symphoricarpos* spp.) and sumac (*Rhus* spp.) are locally abundant.

We examined aerial photographs to select 16 50 × 50 m (0.25-ha) grassland sites that ranged from 0% redcedar cover (herbaceous vegetation without trees) to 76% redcedar cover (closed-canopy redcedar woodlands). According to published ecological site descriptions (Soil Survey Staff 2007), our study sites comprised claypan prairies ($n = 9$), loamy prairies ($n = 6$), and a sandy savanna ($n = 1$) having moderately deep, well-drained upland soils derived from shale and/or sandstone (Appendix A). In addition, because the process of redcedar encroachment occurs within a mosaic of land management regimes, we selected sites characterized by cattle grazing and fire histories typical within the region. Ecological site types and grazing/fire histories were somewhat evenly represented along the gradient of redcedar cover, so we chose to pair our study sites according to their level of redcedar cover, with each site pair differing by <3% redcedar cover (Appendix A). According to tree age estimates, encroachment of these sites had occurred within the past 31–62 years. Study sites were distributed over an area of ~10 000 ha, but the distance between paired sites did not follow any clear trend along the gradient of pretreatment redcedar cover (Appendix A).

We employed a BACI experimental design to address our study objectives, randomly assigning treatments (tree removal, no tree removal) within each pair of sites. However, our study design differed from the classic BACI design in two important ways. First, whereas replicates on the control and treatment sides of the classic BACI design are randomly designated, we paired control and treatment sites according to their level of redcedar cover. Second, the classic BACI design examines the mean difference between all treatment and control samples (e.g., treatment–control) before and after treatment. We examined changes (e.g., after–before) at each particular site within two time intervals ($T_1$–$T_0$ and $T_2$–$T_0$ where $T_0 = 2005$, $T_1 = 2006$, and $T_2 = 2007$), and then examined the difference between the changes that had occurred within each pair of sites along the redcedar cover gradient.

Woody and herbaceous vegetation, terrestrial invertebrates, and small-mammal assemblages were quantified on all sites in 2005. In February 2006, redcedar trees were mechanically removed from each treatment site, and from a 10-m buffer zone immediately surrounding each treatment site. Thus, the total removal area per site was 70 × 70 m (0.49 ha). Removal equipment consisted of a small, rubber-tracked skid-steer vehicle that did not uproot trees, but sheared them at the main stem. All felled trees were transported >30 m from each removal site, and floral and faunal assemblages were subsequently monitored on removal and nonremoval sites for two

years following treatment. Soil penetrometer measurements (in kilograms per square centimeter; Forestry Suppliers, Incorporated, Jackson, Mississippi, USA) made posttreatment on removal and nonremoval sites ($n = 50$ per site) were used to determine the extent to which the tree removal process may have influenced soil compaction.

### *Floral and faunal sampling*

We measured vegetation annually during the three years of our study. We examined herbaceous vegetation in midsummer (15 July–1 August) and determined species composition and canopy cover (modified from Daubenmire 1959) within 16 1-$m^2$ quadrats at each study site (total $n = 256$ quadrats; Appendix B). Visual obstruction (Robel et al. 1970) was used as a proxy for herbaceous vegetation biomass, and visual obstruction measurements ($n = 91$) were collected within a $13 \times 13$ grid having ~3.5-m spacing. We quantified visual obstruction by taking three measurements at each level of visual obstruction and subsequently clipping all vegetation from a 0.25-$m^2$ area directly in front of each measurement. Mean oven-dried mass of vegetation clippings was used to develop an equation predicting herbaceous vegetation biomass from visual obstruction measurements. Canopy cover of woody vegetation was measured using the line-intercept method (Canfield 1941) along four evenly spaced 50-m transects at each study site (Appendix B).

We sampled the terrestrial invertebrate assemblage using pitfall traps annually in July–August of all years. Traps consisted of a plastic cup (100-mm diameter, 150-mm depth) buried flush with the ground surface and filled with ~100 mL of a propylene glycol solution. Eight pitfall traps were arranged in one of two randomly chosen configurations at each study site (Appendix B), and installed >14 m from site edges to focus sampling on resident individuals. We left pitfall traps undisturbed for five consecutive days and subsequently counted and identified all captured invertebrates to taxonomic family. We also determined the total oven-dried mass (±0.1 mg) of all individuals within an invertebrate family at each site.

We sampled the small-mammal assemblage at each study site in spring (May–June), summer (July–August), and winter (December–January) of all years using a $7 \times 7$ grid of Sherman live traps with ~7-m trap spacing (Appendix B). Traps were baited with rolled oats for five consecutive nights and checked each morning. During winter sessions, cotton was used in each trap to provide thermal insulation for captured individuals. We identified all captured small mammals to species, marked each with a unique toe-clip combination, and released individuals at their point of capture. Logistical constraints prevented us from sampling all sites simultaneously. Therefore, we divided sites into four groups based on proximity and sampled each group in random order during each sampling session. To avoid confounding capture results, invertebrate and small-mammal sampling activities were never conducted concurrently at a particular study site. All aspects of animal use were approved by the Southern Illinois University Institutional Animal Care and Use Committee (protocol 05-046).

### *Data analysis*

Shannon's indices of species diversity and evenness ($H$ and $J$, respectively [Begon et al. 2006]) were used for all floral and faunal assemblages, and species richness was determined from species counts. Among herbaceous and woody vegetation assemblages, we determined the relative abundance of each plant species within the quadrat or along the transect where it occurred. Species totals were then pooled across all samples at each site. Redcedar cover was omitted from our analysis of the woody vegetation assemblage. Relative biomass has been shown to be more effective than abundance as a measure of invertebrate compositional changes (Saint-Germain et al. 2007), so we used the relative biomass of each invertebrate family to compute family diversity and richness. Small-mammal abundance was indexed as the number of individuals captured per 100 trap nights after correcting for trapping effort (Nelson and Clarke 1973). Shifts in small-mammal species composition were examined using the change in proportional abundance of woodland- and grassland-associated small mammals along the gradient of pretreatment redcedar cover according to known habitat preferences (Kaufman et al. 1988, Clark et al. 1998, Kaufman et al. 2000).

The SAS/STAT software package (Version 9.1.3; SAS Institute 2004) was used for all statistical analysis. We checked assumptions of normality and heteroscedasticity (PROC UNIVARIATE) prior to analysis and used log-transformation ($\log_{10}[y + 0.1]$) when necessary. Our analytical objective was to determine the influence of pretreatment redcedar cover on floral and faunal responses to tree removal. To accomplish this objective, we determined changes in assemblage characteristics (e.g., mean capture rate, richness, biomass, diversity, and evenness) by subtracting the pretreatment value for each site from values for each year of posttreatment (i.e., $y_{2006} - y_{2005}$ and $y_{2007} - y_{2005}$). Tree removal was not required at 0% redcedar cover, so we pooled values within each year for these sites, and used changes at 0% redcedar sites as an index of background environmental variability. Finally, within each site pair, we subtracted the nonremoval site value from its corresponding removal site value. Thus, we examined trends in the differences between removal and nonremoval sites plotted along the pretreatment redcedar cover gradient. This analytical approach reduced both sample size and statistical power, so we chose to report all results with $P < 0.10$.

We used regression (PROC REG) to determine whether a linear, polynomial, or logarithmic trend described differences between removal and nonremoval

sites in each posttreatment year. We used a transformation ($\log_{10}[x]$) to linearize data for testing the logarithmic trend. We evaluated each model by regressing values for each response variable on the pooled percentage of redcedar cover across each site pair, and determining whether the regression slope was different from zero. A significant regression slope indicated that responses to treatment represented an interaction between redcedar removal and the level of pretreatment redcedar cover. We used Akaike's Information Criterion (AIC; Akaike 1974) to select the top a priori interaction model (i.e., linear, polynomial, or logarithmic; Fig. 1). To examine differences in general site characteristics, or where responses to removal did not exhibit a cover treatment interaction, we used *t* tests (PROC TTEST) to test whether differences between means differed from zero. Finally, we descriptively examined changes in grassland- and woodland-associated small mammals by assigning *Peromyscus maniculatus*, *Chaetodipus hispidus*, *Reithrodontomys fulvescens*, *Reithrodontomys montanus*, and *Sigmodon hispidus* to a grassland group and *Peromyscus leucopus* and *Neotoma floridana* to a woodland group (Clark et al. 1988, Kaufman et al. 1988, 2000).

## Results

### *General site characteristics*

Posttreatment soil penetrometer readings exhibited no trend along the redcedar gradient for removal sites ($P = 0.72$) or nonremoval sites ($P = 0.13$). In addition, *t* tests revealed no differences in penetrometer readings between removal and nonremoval sites ($t_{12} = 0.76$, $P = 0.46$).

### *Floral assemblages*

Herbaceous plant species diversity on removal sites increased relative to nonremoval sites, and this treatment effect interacted with the pretreatment level of redcedar cover (Fig. 2). Differences in herbaceous plant diversity were described by a linear trend (Fig. 2A; $y = -0.67 + 0.02x$, $F_{1,5} = 28.82$, $P < 0.01$, $r^2 = 0.85$) in the first year following treatment (hereafter 2006). This linear model had a $\Delta$AIC = 1.02 lower than the logarithmic model. Differences in herbaceous vegetation diversity followed a polynomial trend (Fig. 2B; $y = -0.79 + 0.05x - 0.0005x^2$, $F_{2,4} = 8.23$, $P = 0.04$, $r^2 = 0.8$) in the second year following treatment (hereafter 2007), with $\Delta$AIC 2.02 lower than that of the logarithmic model, and the greatest differences in diversity being observed at intermediate levels of redcedar cover. Trends in herbaceous plant diversity corresponded more closely to differences in species evenness than to those of species richness (Table 1). Species evenness was best described by a linear trend ($y = -0.11 + 0.003x$, $F_{1,5} = 5.49$, $P = 0.07$, $r^2 = 0.52$) in 2006. This model had a $\Delta$AIC = 0.33 lower than the logarithmic model. Differences in mean evenness were greater at removal sites (+0.019 ± 0.01; mean ± SE) than at nonremoval sites (−0.04 ± 0.02) in 2007 ($P = 0.04$). Herbaceous plant biomass did not vary according to a cover treatment interaction in either 2006 or 2007 ($P = 0.9$ and $P = 0.62$, respectively; Fig. 3A). However, mean differences in herbaceous biomass at removal sites (+1069 ± 373 kg/ha; mean ± SE) were greater than those of nonremoval sites (−1205 ± 151 kg/ha) in 2007 ($P < 0.01$).

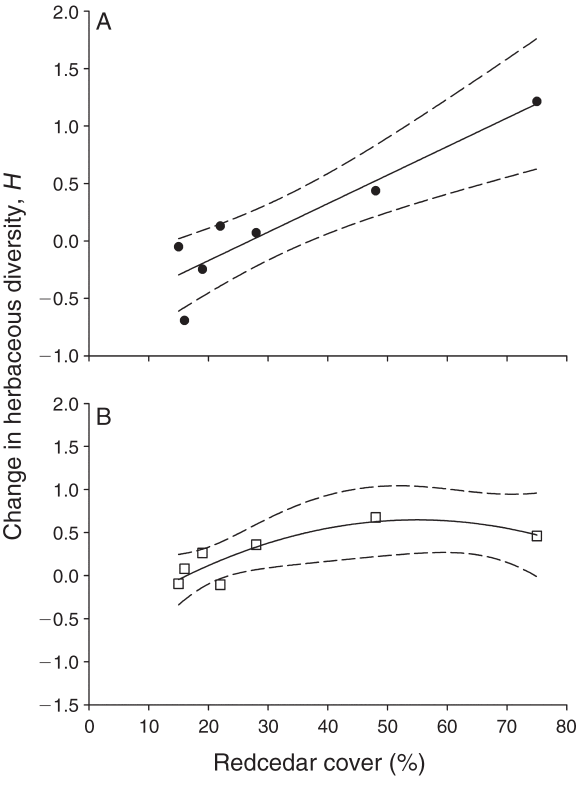


FIG. 2. Differences in herbaceous plant diversity between pairs of sites in north-central Oklahoma, USA, in which redcedar was experimentally removed from one member of each pair. Symbols illustrate differences (A) one year and (B) two years following redcedar removal. Regressions are shown as solid lines and are bounded by dashed lines (95% confidence intervals).

Woody plants responded to redcedar removal differently one and two years after treatment. Woody plant diversity varied by a cover treatment interaction in 2006, with differences between removal and nonremoval sites exhibiting a curvilinear increase along the pretreatment cover gradient (Fig. 3B). A polynomial model provided the best fit for trends in woody plant diversity along the pretreatment cover gradient (closest $\Delta$AIC = 5.42). This model indicated that the woody diversity response had its greatest values occurring at the upper extreme of the redcedar gradient ($y = 0.49 - 0.42x + 0.0008x^2$, $F_{2,4} = 22.53$, $P < 0.01$, $r^2 = 0.92$). In 2007, no cover treatment interaction effects were present and linear, polynomial, and logarithmic models were unable to describe trends

TABLE 1. Changes in species evenness and richness of herbaceous plant, woody plant, and small-mammal assemblages in two years following experimental redcedar removal on grassland sites in north-central Oklahoma, USA.

| Assemblage | Pretreatment redcedar cover (%)† | Evenness, *J* | | Richness, *S* | |
|---|---|---|---|---|---|
| | | 2006 | 2007 | 2006 | 2007 |
| Herbaceous plants | 15 | 0.003 | −0.02 | −2 | −1 |
| | 16 | −0.18 | 0.01 | −5 | −2 |
| | 19 | −0.01 | 0.08 | −5 | 6 |
| | 22 | 0.04 | −0.05 | 0 | 6 |
| | 28 | −0.04 | 0.15 | 7 | −7 |
| | 48 | 0.02 | 0.14 | 11 | 5 |
| | 75 | 0.15 | 0.13 | 18 | 7 |
| Woody plants | 15 | −0.01 | −0.02 | 2 | −1 |
| | 16 | 0.31 | 0.18 | −4 | −5 |
| | 19 | −0.02 | 0.21 | 0 | −1 |
| | 22 | −0.12 | 0.01 | 3 | 3 |
| | 28 | −0.03 | 0.29 | −1 | 2 |
| | 48 | 0.37 | 0.04 | −2 | −4 |
| | 75 | 0.76 | 0.41 | 4 | 1 |
| Small mammals | 15 | 0.15 | −0.04 | 1 | 3 |
| | 16 | −0.14 | 0.06 | 0 | 2 |
| | 19 | −0.19 | 0.34 | 0 | 0 |
| | 22 | −0.38 | −0.2 | 3 | 3 |
| | 28 | −0.1 | −0.11 | 3 | 4 |
| | 48 | 0.28 | 0.01 | 1 | 2 |
| | 75 | 0.41 | 0.24 | 1 | 2 |

*Note:* Data represent differences between pretreatment (2005) and posttreatment (2006 or 2007) values corrected by similar differences on paired, nonremoval sites.

† Paired sites differed pretreatment by <3% redcedar cover.

along the pretreatment cover gradient ($P = 0.38$, $P = 0.21$, and $P = 0.51$, respectively). In addition, no difference existed ($P = 0.39$) between mean changes in woody plant diversity between removal (+0.26 ± 0.08; mean ± SE) and nonremoval (+0.12 ± 0.13) sites. Trends in woody plant diversity in 2006 corresponded more closely to differences in woody plant species evenness than to species richness, especially at higher levels of pretreatment redcedar cover (Table 1). Woody plant evenness exhibited a cover treatment interaction in 2006, with differences between removal and nonremoval sites described by a linear trend ($y = -0.2 + 0.01x$, $F_{1,5} = 12.93$, $P = 0.02$, $r^2 = 0.72$). This linear model exhibited $\Delta AIC = 0.24$ from the polynomial model. However, in 2007, no linear, polynomial, or logarithmic trends were evident ($P = 0.19$, $P = 0.36$, and $P = 0.23$, respectively), although mean evenness was higher ($P = 0.03$) at removal sites (+0.29 ± 0.04) than at nonremoval sites (+0.13 ± 0.05).

### *Faunal assemblages*

We captured 47 165 invertebrates representing 103 taxonomic families over the course of our study (Appendix C). Pitfall traps at the 22% level of pretreatment cover were damaged by wildlife during data collection, preventing us from analyzing changes at this pair of sites. In general, terrestrial invertebrate responses to treatment were only evident in the first year following tree removal. Changes in invertebrate family richness were best described by a linear trend ($y = -22.2 + 0.57x$, $F_{1,4} = 5.9$, $P = 0.07$, $r^2 = 0.6$) in 2006, indicating a cover treatment interaction (Fig. 4A), with a $\Delta AIC = 0.38$ between this model and the logarithmic model. Invertebrate family richness did not follow a clear trend in 2007. Post hoc correlations revealed that at removal sites, changes in invertebrate family richness were strongly associated with changes in herbaceous and woody diversity in 2006 ($r = 0.98$, $P < 0.01$, and $r = 0.82$, $P = 0.05$, respectively) but not in 2007 ($r = 0.62$, $P = 0.19$ and $r = 0.57$, $P = 0.24$, respectively). Total invertebrate biomass varied by a cover treatment interaction in 2006, and a polynomial model ($y = -0.2 - 0.03x + 0.0006x^2$, $F_{2,3} = 15.73$, $P = 0.03$, $r^2 = 0.91$; Fig. 4B) exhibited the lowest AIC, being 2.73 lower than the linear model. The polynomial trend was bimodal with the highest values occurring at the highest level of pretreatment redcedar cover. In 2007, total invertebrate biomass did not follow a clear trend, and mean differences in biomass at removal sites (−0.61 ± 0.21; mean ± SE) did not differ ($P = 0.23$) from those at nonremoval sites (−0.19 ± 0.25). Correlations conducted post hoc revealed that changes in herbaceous and woody diversity were associated with changes in invertebrate biomass in

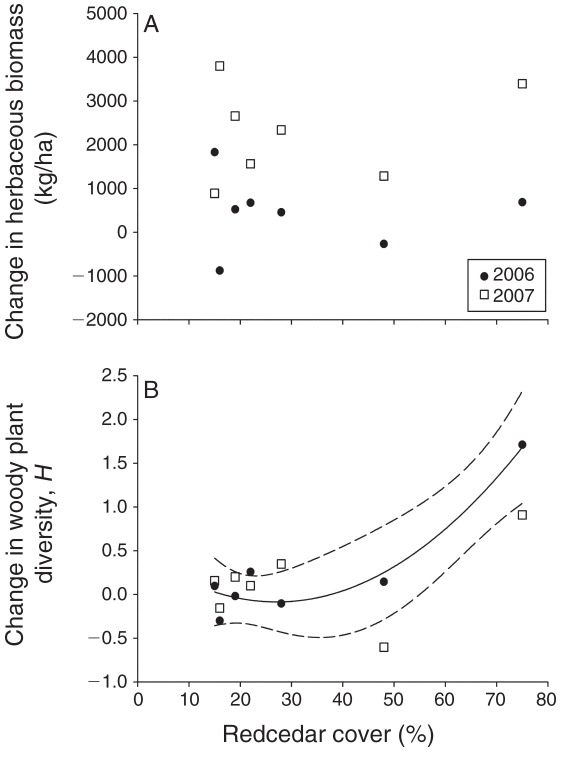


FIG. 3. Differences in (A) herbaceous plant biomass and (B) woody plant diversity between pairs of sites in north-central Oklahoma, USA, in which redcedar was experimentally removed from one member of each pair. Symbols illustrate paired differences one year (2006) and two years (2007) following redcedar removal. The regression describes 2006 woody diversity data and is shown as a solid line bounded by dashed lines (95% confidence intervals). In 2007, no cover treatment interaction effects were present.

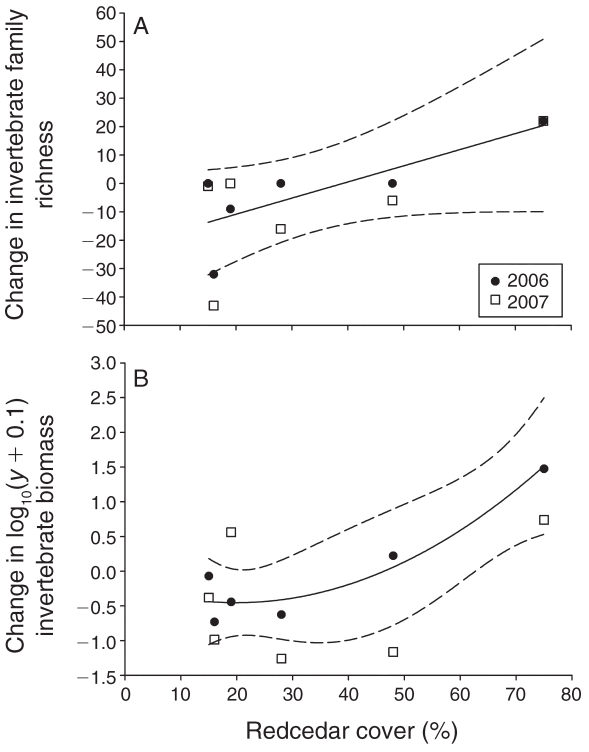


FIG. 4. Differences in (A) terrestrial invertebrate family richness and (B) total log-transformed invertebrate biomass ($y + 0.1$, with biomass measured in grams) between pairs of sites in north-central Oklahoma, USA, in which redcedar was experimentally removed from one member of each pair. Symbols illustrate paired differences one year (2006) and two years (2007) following redcedar removal. Regressions describe 2006 data for both panels and are shown as solid lines bounded by dashed lines (95% confidence intervals). Invertebrate family richness and biomass did not follow clear trends in 2007.

2006 ($r = 0.84$, $P = 0.04$, and $r = 0.97$, $P < 0.01$, respectively), but not in 2007 ($r = 0.07$, $P = 0.89$, and $r = 0.67$, $P = 0.14$, respectively).

We recorded 1562 captures of 10 small-mammal species over 32 593 trap nights. We only captured six individuals representing three species (*Blarina hylophaga*, *Microtus ochrogaster*, and *Mus musculus*), so we excluded these from all analyses. In addition, three other species (*Chaetodipus hispidus*, *Neotoma floridana*, and *Reithrodontomys montanus*) composed <6% of the captured population. We included these three species in measurements of species richness, evenness, diversity, and species composition, but were unable to analyze trends in individual species abundance due to low sample sizes.

Small-mammal species diversity varied according to a cover treatment interaction in 2006, with small-mammal diversity following a logarithmic trend ($y = -1.38 + 1.16x$, $F_{1,5} = 6.73$, $P = 0.05$, $r^2 = 0.57$). This model had a $\Delta AIC = 0.57$ from the linear model. No clear trends were evident in 2007, although diversity was higher ($P < 0.01$; Fig. 5A) at removal sites (+0.29 ± 0.11; mean ± SE) than at nonremoval sites (+0.23 ± 0.09). No significant association was found in post hoc correlations of small-mammal diversity and herbaceous plant biomass in 2006 ($r = 0.31$, $P = 0.5$) or 2007 ($r = -0.54$, $P = 0.21$). However, small-mammal diversity was strongly associated with herbaceous plant diversity in 2006 ($r = 0.85$, $P = 0.02$), although not in 2007 ($r = 0.07$, $P = 0.88$). Differences in small-mammal diversity were more closely associated with changes in species evenness rather than species richness (Table 1). Small-mammal species evenness varied according to a cover treatment interaction, following a logarithmic trend ($y = -1.07 + 0.75[\log_{10}x]$, $F_{1,5} = 4.62$, $P = 0.08$, $r^2 = 0.48$) in 2006 that had a $\Delta AIC = 0.46$ lower than the linear model. No clear trends in small-mammal evenness were evident in 2007. Small-mammal species richness did not exhibit cover treatment interactions in 2006 or 2007, although mean richness was higher at removal sites compared with nonremoval sites in 2006 ($P = 0.02$) and 2007 ($P < 0.01$).

Capture rates of the four most common small-mammal species varied widely in the two years following

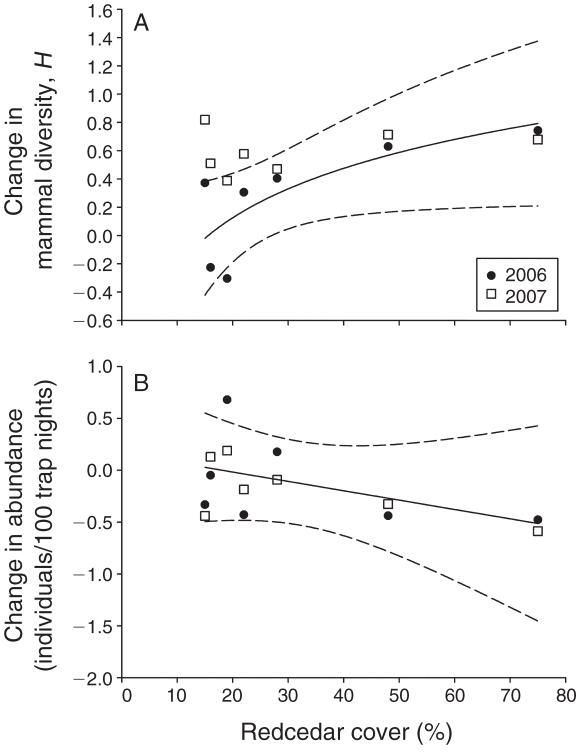


FIG. 5. Differences in (A) small-mammal diversity and (B) *Peromyscus leucopus* (white-footed mouse) abundance between pairs of sites in north-central Oklahoma, USA, in which redcedar was experimentally removed from one member of each pair. Symbols illustrate paired differences one year (2006) and two years (2007) following redcedar removal. Regressions describe 2006 small-mammal diversity and 2007 *P. leucopus* abundance, and are shown as solid lines bounded by dashed lines (95% confidence intervals). No significant trends were evident for small-mammal diversity in 2007 or *P. leucopus* abundance in 2006.

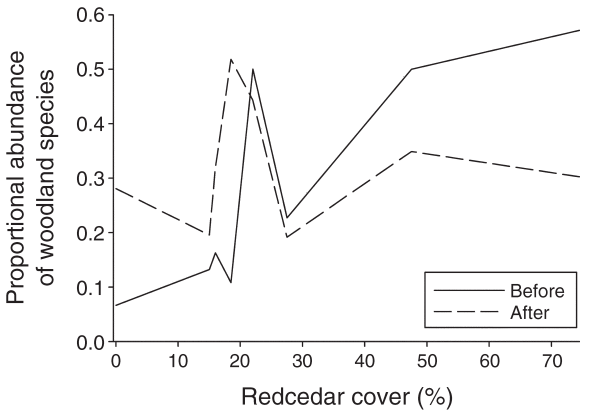


FIG. 6. Proportional abundance of woodland- and grassland-associated small mammals captured on eight sites in north-central Oklahoma, USA, along a gradient of redcedar encroachment before and after experimental redcedar removal.

tree removal (Appendix D). *P. leucopus* was the most frequently captured small-mammal species in the study. Although mean abundance of *P. leucopus* exhibited no clear trend in 2006, its abundance declined to a greater degree at removal sites than at nonremoval sites along the redcedar gradient in 2007. Differences in *P. leucopus* abundance were described by a linear trend ($y = 0.09 - 0.009x$, $F_{1,5} = 4.07$, $P = 0.09$, $r^2 = 0.45$; Fig. 5B). Abundance of *P. maniculatus*, *R. fulvescens*, and *S. hispidus* exhibited no clear trends in either 2006 or 2007, and we found no differences in mean small-mammal abundance between removal and nonremoval sites in either 2006 or 2007.

The proportional abundance of woodland- and grassland-associated small mammals changed following the removal of redcedar on treatment sites. Grassland-associated small mammals increased following tree removal, with the greatest increases occurring at the highest levels of pretreatment redcedar cover. For example, at the most heavily encroached site (75% pretreatment redcedar cover), tree removal led to a 27% increase in the proportion of grassland-associated small mammals (Fig. 6).

## DISCUSSION

Woody encroachment by *Juniperus* species has been associated with decreased species richness and diversity of grassland-associated flora and fauna (Bragg and Hulbert 1976, Horncastle et al. 2005), and mechanical tree removal can be an effective, albeit intensive, technique for increasing grassland diversity in areas undergoing encroachment (Bates et al. 2000, Ansley et al. 2006). In our study, floral and faunal responses to tree removal increased linearly or logarithmically toward the highest levels of pretreatment redcedar cover (Table 2). However, in some cases, removal of redcedar promoted responses that were accentuated at the highest levels of the pretreatment cover gradient. Our study demonstrated the important influence of pretreatment redcedar cover on floral and faunal responses to tree removal, and found mixed evidence for a system parameter shift (sensu Beisner et al. 2003) associated with high levels of redcedar cover in the two years following tree removal.

### *Floral assemblages*

High levels of encroachment by woody plants have been associated with persistent alterations to the abiotic environment (Schlesinger et al. 1990, Hibbard et al. 2001, Jackson et al. 2002), and tree-removal studies in grasslands encroached by *Cornus drummondii* have documented biotic legacy effects that delayed posttreatment grassland recovery (Lett and Knapp 2003). In areas of *Juniperus* encroachment, increases in tree cover alter species composition and decrease biomass among herbaceous plants (Engle et al. 1987, Gehring and Bragg 1992, Miller et al. 2000), and increase nutrient accumulation (i.e., carbon and nitrogen) both in plant biomass and soil beneath the canopy (Norris et al. 2001, Smith and Johnson 2004, McKinley and Blair 2008). Interactions of these biotic and abiotic factors influence the trajectory of responses to tree removal. Our study corresponds to other studies showing relatively rapid increases in herbaceous diversity and cover following tree removal (Bates et al. 2000, Brudvig and Asbjornsen 2009), and the trends we note suggest that changes in herbaceous diversity are strongly influenced by the level of pretreatment redcedar cover (Fig. 1).

Changes in herbaceous plant diversity following treatment were likely influenced by the spatial distribution of redcedar and herbaceous cover along the gradient of woody cover. At lower levels of encroach-

TABLE 2. Summary of floral and faunal responses to experimental redcedar removal along a gradient of redcedar encroachment in north-central Oklahoma, USA.

| Assemblage | Response | Alternative supported | |
|---|---|---|---|
| | | 2006 | 2007 |
| Herbaceous plants | diversity | B, C† | C |
| | evenness | B, C† | C |
| | biomass | Ø | A |
| Woody plants | diversity | C | Ø |
| | evenness | B, C† | A |
| Terrestrial invertebrates | family richness | B, C† | Ø |
| | total biomass | C | Ø |
| Small mammals | diversity | B, C† | A |
| | evenness | B, C† | Ø |
| *Peromyscus leucopus* | abundance | Ø | B |
| *Peromyscus maniculatus* | abundance | Ø | Ø |
| *Reithrodontomys fulvescens* | abundance | Ø | Ø |
| *Sigmodon hispidus* | abundance | Ø | Ø |

*Note:* Alternative hypotheses were: Ø, no detectable response; A, null response to removal; B, linear response to biotic factors along redcedar gradient; C, nonlinear response to biotic–abiotic interaction along redcedar gradient. See Fig. 1.

† Models within two AIC units of one another.

ment, individual trees tend to be isolated within a spatially homogeneous matrix of herbaceous plant cover. However, at higher levels of redcedar cover, herbaceous vegetation becomes confined to small patches between clumps of redcedar trees. Limb et al. (2010) noted that the effect of increasing redcedar cover on herbaceous vegetation was a function of the area occupied by redcedar, with decreases in herbaceous diversity generally restricted to the area beneath the canopy. In our study, as the level of pretreatment redcedar cover increased, tree removal exposed a larger number of patches that were practically devoid of aboveground vegetation, near herbaceous plant patches and seed sources, and received plentiful solar radiation. These conditions facilitated increases in herbaceous diversity. This effect was evident in the linear trend we noted in 2006, suggesting that the response of herbaceous plants to tree removal was maximized at the highest levels of pretreatment redcedar cover.

Herbaceous plant diversity along the redcedar gradient in 2007 increased, then attenuated beyond 28% pretreatment cover; and this asymptotic effect appeared to correspond to a temporal shift in herbaceous species composition. Given the proportion of newly opened patches at the highest level of pretreatment cover following tree removal, the presence of early-successional herbaceous species, many of which were annuals, tended to increase diversity in 2006. However, in 2007 this effect was diminished as annuals began to be replaced by a mixture of native grasses and forbs, both generalists and grassland specialists, that had been present prior to tree removal (R. Limb, *unpublished data*). Changes in diversity in 2007 tended to be associated with slight increases in species richness and species evenness (Table 1). Similar patterns of succession among functional groups of herbaceous plants in the years following woody plant removal have been observed in other encroached systems (Bates et al. 2005, Lett and Knapp 2005).

Interestingly, one removal site at the low end of the pretreatment redcedar gradient exhibited appreciably lower diversity compared with its corresponding nonremoval site in 2006 and 2007 (Fig. 2). At this site, a nonnative plant species (*Lespedeza cuneata*) occupied the periphery of patches opened by redcedar removal. *L. cuneata* can decrease establishment of other plant species through shading (Brandon et al. 2004), and it is likely that *L. cuneata* abundance hindered the rate of reestablishment by other herbaceous plant species following removal. In addition, this site was one of the most continuously grazed of our study sites within the past two decades (Appendix A), which may have contributed to its attenuated response to redcedar removal.

The lack of an increase in herbaceous plant biomass in 2006 (Fig. 3A), despite the increase in plant diversity following treatment, suggested that plant recolonization of patches opened by tree removal may have occurred rapidly, but that herbaceous plants had not added appreciable biomass until the year following their initial establishment. This result is consistent with a compositional shift from annual to perennial grasses and forbs within two years following redcedar removal. In addition, similar studies have noted that increases in herbaceous biomass following *Juniperus* removal were only significant after multiple growing seasons (Bates et al. 2005, Ansley et al. 2006).

Responses of the herbaceous community to redcedar removal also occurred within the context of larger-scale climatic events. During the 2006 water year (1 October 2005–30 September 2006), the central region of Oklahoma received 60% of normal precipitation, whereas in 2007, this region received 144% of normal precipitation, the greatest water-year rainfall in the previous 87 years (Rainfall and Drought Update 2008). As a result, herbaceous plant production was elevated in 2007 relative to 2006 across the redcedar cover gradient (Fig. 3A).

Our results suggest that competitive interactions among woody and herbaceous plants, combined with variable climatic conditions, influenced responses of woody plants to redcedar removal. A variety of subdominant shrubs and trees (e.g., *Cornus*, *Ulmus*, *Quercus*, *Symphoricarpos*) commonly occur in redcedar-encroached grasslands. Although redcedar tended to compose a greater proportion of the woody plant assemblage at higher levels of pretreatment cover, this increase was not accompanied by a decrease in the number of woody plant species. Removal of redcedar presumably released these other woody species from a major source of competition, and this effect was particularly evident at sites having high levels of pretreatment cover (Fig. 3B). In contrast, at lower levels of pretreatment cover, redcedar made up a smaller proportion of the woody community, and the effect of tree removal on the woody plant assemblage was less evident. In addition, plentiful precipitation and a corresponding increase in herbaceous plant biomass in 2007 may have negatively affected woody plant responses to tree removal (Fig. 3B).

### *Faunal assemblages*

Interpretation of changes within the invertebrate assemblage following removal is difficult. Invertebrate abundance and taxonomic composition in grassland and woodland ecosystems are known to vary widely in response to changes in precipitation, temperature, plant biomass, and land management (Jonas et al. 2002, Saint-Germain et al. 2005). Invertebrates are closely tied to changes in plant species diversity and structural complexity (Dennis et al. 1998, Siemann et al. 1998), and although not always reaching significance, our post hoc analyses were consistent with these findings in 2006. As an example, the combined effect of heavy grazing (Appendix A) and presence of an exotic plant at the 16% redcedar cover site decreased herbaceous and woody

plant diversity and associated biomass and richness of the invertebrate assemblage. Losses in invertebrate family richness and biomass were noted on most redcedar removal sites in 2006 and 2007, and appeared to follow changes in herbaceous and woody plant diversity. In addition, losses of invertebrate biomass on removal relative to nonremoval sites were associated with changes in the occurrence of some proportionately larger-bodied invertebrate taxa (e.g., Orthoptera, Coleoptera) from year to year. We speculate that perhaps the combined effects of tree removal and the extreme and contrasting precipitation of both years negatively impacted invertebrate assemblages on removal sites more strongly than on nonremoval sites.

Small-mammal distribution in grasslands is a function of variation in herbaceous diversity and biomass (Grant and Birney 1979, Clark et al. 1998), and this assemblage is strongly influenced by management of woody plant species (Baker and Frischknecht 1973, Severson 1986). In areas of redcedar encroachment, small-mammal diversity and abundance may be maximized at intermediate levels of cover (Matlack et al. 2008, Alford 2009). Nevertheless, we noted a logarithmic response of small-mammal diversity to removal along the redcedar gradient in 2006, and an across-the-board increase in 2007. Although our post hoc correlations revealed that small-mammal diversity did not follow changes in herbaceous biomass, changes in small-mammal diversity were strongly associated with changes in herbaceous diversity, at least in 2006. In addition, comparing trends of plant and small-mammal diversity along the pretreatment redcedar gradient suggests that small-mammal responses are more strongly tied to changes in herbaceous rather than woody plant diversity (Figs. 2A, 5A). Our results underscore the importance of vegetation shifts for rapidly influencing the relative abundance of grassland- and woodland-associated small mammals in prairies (Horncastle et al. 2005), as removal of woody plants can increase abundance and promote compositional shifts toward a grassland-associated small-mammal assemblage (Baker and Frischknecht 1973, McMurry et al. 1994).

Climatic events can have an important effect on small-mammal population and community parameters by altering available food supply or changing dominant vegetation structure (Yahner 1991, Lewellen and Vessey 1998). Letnic et al. (2005) noted the importance of a pulsed climatic event (La Niña–El Niño southern oscillation) for explaining responses of small-mammal assemblages to vegetation change following wildfire. In the present study, the relative drought conditions of 2006, followed by copious precipitation in 2007, influenced both the vegetation and consumer communities. Drought in 2006 appears to have muted some responses to cedar removal (e.g., herbaceous biomass), whereas the climate in 2007 may have been responsible for homogenizing responses to treatment (e.g., herbaceous biomass, small-mammal diversity) along the gradient of pretreatment redcedar cover.

### *Conclusions*

Managing woody plant species in grassland systems will require a suite of techniques that integrate the level of woody cover, management regime, climatic variability, and various life-history traits of the encroaching species. Many species resprout following removal (Lett and Knapp 2005, Ansley et al. 2006), are dispersed by animal guilds at different stages of encroachment and spatial scales (Archer et al. 1988, Horncastle et al. 2004), and have the capacity to alter important abiotic parameters (Schlesinger et al. 1990, Hibbard et al. 2001). In our system, state-variable shifts appeared to characterize the shift from grassland to redcedar woodland (Limb et al. 2010). Experimental redcedar removal initiated a switch (sensu Petraitis and Latham 1999) back to a grassland state that was evident in both flora and fauna. The level of pretreatment encroachment did not constrain this switch, and, for some floral and faunal metrics, actually facilitated it (Table 2). However, given the relatively short time frame of this study, the persistence of this state awaits further investigation. Frequent fire is the primary factor in our system limiting the influx of woody plants, but is rendered ineffective by such processes as heavy grazing and increased prairie fragmentation (Briggs et al. 2005). Research in grassland systems encroached by woody species must continue to identify the diverse drivers and complex interactions that facilitate encroachment and maintain alternate states. Given the historic degradation of grasslands and savannas, their degree of anthropogenic fragmentation, and the endangered flora and fauna that reside there, decisive management action will be necessary to conserve these imperiled ecosystems.

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## Supplemental Material

### Appendix A

General characteristics of eight pairs of grassland sites studied from 2005 to 2008 in north-central Oklahoma, USA (*Ecological Archives* A022-052-A1).

### Appendix B

Schematic of a 0.25-ha study site illustrating the locations of small-mammal traps, two configurations of invertebrate pitfalls, vegetation line transects, and herbaceous plant sampling quadrats (*Ecological Archives* A022-052-A2).

### Appendix C

Taxonomic orders, represented families, and total abundance of terrestrial invertebrates collected at eight pairs of grassland sites from 2005 to 2008 in north-central Oklahoma, USA (*Ecological Archives* A022-052-A3).

### Appendix D

Mean capture rates of the four most commonly captured small-mammal species one year before and two years following experimental redcedar removal in north-central Oklahoma, USA (*Ecological Archives* A022-052-A4).